

Balancing predator avoidance with hunting opportunities: substrate choice by *Misumena vatia* spiderlings

Youssef Garcia-Bengochea and Douglass H. Morse¹: Department of Ecology & Evolutionary Biology, Box G-W, Brown University, Providence, RI 02912, USA

Abstract. When crab spiderlings *Misumena vatia* (Clerck 1757) emerge from their natal nests their small resource reserve makes them vulnerable to starvation, while their small size makes them vulnerable to many predators. Choosing substrates that allow hunting opportunities as well as protection from predators may thus be life or death decisions. Here we investigate the substrate choice of crab spiderlings on goldenrod *Solidago canadensis* and *Solidago juncea* inflorescences in relation to a frequently encountered predator, the jumping spider *Pelegrina insignis* (Banks 1892). Flower heads of *S. canadensis* are smaller and more densely packed on branches of the inflorescences than the heads of *S. juncea*, but the two species attract similar numbers of small flies, the major prey of the spiderlings and jumping spiders. Crab spiderlings significantly preferred *S. canadensis*, both in initial choice and length of time occupied, as did their jumping spider predator. However, capture times of spiderlings by small jumping spiders (< 5 mg) did not significantly differ on the two goldenrods, although the preferred goldenrod, *S. canadensis*, provided superior protection from larger jumping spiders (>5 mg). Thus, although occupancy on the preferred goldenrod does not make spiderlings safer from all jumping spiders, it provides superior protection from large ones and may be the basis for the substrate preference of the spiderlings.

Keywords: Crab spider, foraging, jumping spider, *Pelegrina insignis*, Salticidae, Thomisidae

When selecting an appropriate foraging site, an individual should, if possible, choose an area that provides abundant resources (maximizing benefit) and a low risk of predation (minimizing cost) (Lima & Dill 1990; Dukas 1998). Unfortunately for the forager, abundant resources may attract that forager's predators as well, either directly to the resource or to the foragers frequenting it. Animals may make distinct choices between substrates with relatively similar but subtly different characteristics, and these decisions may have important consequences for their survival and growth (Morse 2007).

In this study we evaluate the substrate choices (flowers) made by newly-emerged second-instar crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae), henceforth spiderlings, in relation to availability of prey and the danger resulting from their most common predator, the jumping spider *Pelegrina insignis* (Banks 1892) (Salticidae) (Morse 1992, 2007) on these sites. As soon as the spiderlings emerge from their natal nests during late summer, they become part of the jumping spiders' prey, although the jumping spiders also capture many of the same small insects that constitute the spiderlings' diet.

Spiderlings leave their nests in their second instar and begin hunting immediately. Since they have only recently ventured outside their natal nest, experience plays little or no role in site selection at this time. Spiderlings prefer goldenrod (*Solidago* spp.) as a foraging substrate to other flowers (Morse 2000a, 2005), but the interspecific variation in inflorescence structure and flower head sizes (Semple & Cook 2006) provide a range of both hunting and hiding sites available for small prey (primarily small Diptera) and small predators. To test such variation, we compared the availability of prey and vulnerability of newly emerged spiderlings on two common goldenrod species: *S. canadensis* and *S. juncea*, species whose size and packing of flower heads on an inflorescence differ quantitatively.

Jumping spiders possess a highly developed sense of sight (Jackson & Pollard 1996), which makes concealment especially important to the spiderlings. Jumping spiders of different sizes

even within a species exhibit different levels of maneuverability in these inflorescences as a consequence of the size and spacing of the flower heads (see below) and, likely, their ability to find spiderlings. We treat spiderling size variation as negligible since they are of similar age and relatively small in relation to their substrate and in relation to their jumping spider predators.

Here we investigate whether the goldenrod species favored by the spiderlings will 1) provide the safest inflorescence structure and/or 2) the most favorable hunting site. We predicted that small jumping spiders (2–3 times the mass of spiderlings) would be more dangerous to the spiderlings than larger ones by virtue of their superior maneuverability within the small inflorescence structures. Thus we asked the following questions: Do spiderlings prefer one goldenrod over another (flower choice)? Do spiderlings remain on one goldenrod species longer than another (higher site fidelity)? Do jumping spiders follow the same pattern of use? Does one goldenrod species provide more safety than the other in the presence of predators? Does one goldenrod species provide more food than the other? If one goldenrod species is safer, is that consistent with spiderling preference? How does jumping spider size affect the vulnerability of spiderlings?

METHODS

Study area and vegetation.—We carried out this study in a 3.5 ha field during July–August 2007 and 2008 at the Darling Marine Center of the University of Maine, South Bristol, Lincoln Co., Maine USA (43.57°N, 69.33°W). The field, mown in October but otherwise unmanaged, contains several grasses (Gramineae) and interspersed forbs. During late summer the principal blooming flowers consist of goldenrods (*Solidago* spp.) and asters (*Aster umbellatus*) (Morse 2005). Goldenrods are dominant plants in many old-field communities. In the study area different species of goldenrod produce flowering stems ranging from 0.5 to 1.5 m in height, culminating in large pyramidal inflorescences, with flower heads clustered along several relatively horizontal branches.

¹Corresponding author. E-mail: d_morse@brown.edu

Solidago canadensis is the most common goldenrod in the study area. Its flower heads average 4.1 ± 0.10 mm (mean \pm SE) in height and 2.3 ± 0.05 mm in diameter, with a density of 19.4 ± 2.33 flower heads cm^{-1} ($n = 10$). The next most common goldenrod species in bloom at this time, *S. juncea*, has larger flower heads, 5.6 ± 0.12 mm in height and 3.1 ± 0.09 mm in diameter, and a lower density of 14.2 ± 1.6 flower heads cm^{-1} ($n = 10$). The space between the *S. juncea* flower heads is thus 1.4 ± 0.16 times greater than that of *S. canadensis*, making flower-head density a potentially important factor for both the spiderlings and their variably-sized jumping spider predators (Morse 2006, pers. observ.).

Spiders.—Newly emerged spiderlings weigh from 0.4 to 0.7 mg, most of them from 0.5 to 0.6 mg (Morse 1993). As the spiderlings emerge from their nests, they immediately begin to seek a suitable hunting substrate (Morse 2005). Small jumping spiders, the commonest predators of the spiderlings at this time (Morse 1992), weigh between 0.9 and 10 mg, depending on their instar. Of the small jumping spiders in the study area, *P. insignis* is the most common, making up 88% of the small jumping spiders on goldenrods during this period (Morse 2006). We used *P. insignis* in all of the experiments.

Acquisition of spiders.—Spiderling broods were obtained from nests collected from the field a few days before emergence and used within two days of emergence to minimize possible effects of variability resulting from age, hunger, or experience. Jumping spiders were collected from goldenrod inflorescences throughout the field and from neighboring goldenrod patches.

Time on the two goldenrods.—To determine how long spiderlings and jumping spiders would remain on the two goldenrod inflorescences in the field, we ran four retention tests: *M. vatia* on *S. canadensis*, *M. vatia* on *S. juncea*, *P. insignis* on *S. canadensis*, and *P. insignis* on *S. juncea*. We first lightly dusted the subjects with red powdered micronite dye to distinguish them from others in the field (Morse 2000a). Previous studies have shown that this treatment does not affect the behavior of these spiderlings and small jumping spiders or increase their risk of predation (Morse 2000a, 2006).

We placed the spiderlings and jumping spiders on goldenrod inflorescences, subsequently censusing the inflorescences, one at a time, by visual inspection. If we did not find the individuals by visual inspection, we lightly tapped the entire inflorescence against a white clipboard to dislodge any hiding individuals, subsequently returning them back to the inflorescence. This procedure does not significantly affect the probability of finding the spiderling on a subsequent visit (Morse 2000a). Each census began at approximately 11:00 and ran until 18:00 of that day. We censused the spiderlings each hour, and jumping spiders each half-hour, for the first two hours, to accommodate for the jumping spiders' occasional rapid departure. We then censused all individuals hourly. Individuals that left the substrate immediately were removed from the data set.

Selection of flower heads.—To test further which goldenrod the crab spiders preferred, we made equal-sized blooming branches of the two goldenrods into small bouquets. Using a fine-tipped brush in the laboratory, we placed the spiderlings with their left legs on one goldenrod species and the right ones on the other (Morse 2005). After 30 min we recorded which

flower species the spiderling had selected. Following each run we provided fresh branches and switched the position of the two goldenrod species to control for any variation in the light source. Morse (2005) describes this setup in greater detail. Additionally, to test whether tactile stimulation of the stem explained the spiderlings' choice we repeated the same flower selection procedure but removed the inflorescences, leaving only the stems. This test allowed us to establish the role of the stem, the initial point of contact for many spiderlings, in determining their choice of inflorescences.

Prey visitation to goldenrod inflorescences.—In order to compare the availability of potential prey visiting the two goldenrod species, we counted the number of small dipterans, the major prey of the spiderlings (Morse 2005, 2006) at inflorescences of the two goldenrods during mid-day on 11 days spaced through the study period (maximum of 10 *S. juncea* and 5 *S. canadensis* inflorescences). We also measured the size of the inflorescences of the two species, estimated as the volume of a cone. All counts were made on adjacent pairs of inflorescences in order to provide as direct a comparison as possible.

Predation on flower heads.—We used paired sets of Petri dishes (9 cm diam) as arenas to test the safety of spiderlings on flower heads of the two goldenrod species. Each Petri dish contained part of an inflorescence branch of *S. canadensis* or *S. juncea*. We placed a spiderling on the inflorescence in each Petri dish and allowed it 2 min to settle among the flower heads before placing a jumping spider of known mass (range = 1.0–11.9 mg) in the Petri dish. The jumping spiders had been starved for two days to ensure that they would be adequately hungry to hunt. We ran each trial for 8 h, checking the Petri dishes every 30–60 min to record predation times.

Voucher specimens were placed in the American Museum of Natural History, New York, and the Florida State Collection of Arthropods, Gainesville, Florida.

RESULTS

Time on the two goldenrods.—Spiderlings introduced to inflorescences of the two goldenrod species remained significantly longer on *S. canadensis* than on *S. juncea* (Fig. 1: $t_{123} = 7.32$, $P < 0.0001$ in two-tailed t -test). Jumping spiders introduced to the goldenrod inflorescences also remained significantly longer on *S. canadensis* than on *S. juncea* (Fig. 1: $t_{38} = 3.00$, $P < 0.005$).

Selection of flower heads.—When given a choice between *S. canadensis* and *S. juncea* in the laboratory tests, 80% of the spiderlings (32 of 40) chose *S. canadensis* and 20% (8 of 40) chose *S. juncea*, a highly significant difference ($X^2_1 = 14.40$, $P < 0.001$ in a X^2 one-sample test). In a further effort to test choice, we ran a second trial, simultaneously exposing individuals to the stems of *S. canadensis* and *S. juncea* ($n = 10$). All individuals tested continually moved freely between the two stems, clearly demonstrating that they did not distinguish between the two goldenrods on the basis of their stems, but on the inflorescences themselves.

Prey visits to the goldenrod inflorescences.—Inflorescences of *S. juncea* averaged 46.4% larger than those of *S. canadensis* (1986 ± 291.0 SE cm^3 vs 1064 ± 202.4 cm^3). When corrected for inflorescence size, visitation of prey to the two goldenrods did not differ significantly (*S. juncea* = 0.6 ± 0.13 SE, *S.*

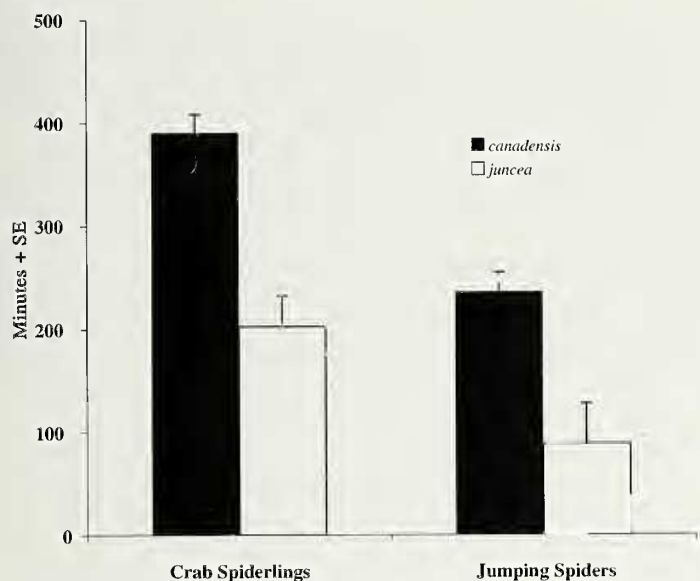


Figure 1.—Length of time (mean \pm SE) spiders remained on goldenrod. White bars = *S. juncea*, $n = 60, 15$; Black bars = *S. canadensis*, $n = 65, 25$.

canadensis = 0.7 ± 0.13 SE prey per inflorescence; $t_{21} = 0.638$, $P > 0.5$ in a two-tailed t -test for the difference between two means). However, evaluating prey in terms of number per inflorescence rather than per inflorescence area would favor *S. juncea* over *S. canadensis* as the more productive substrate ($t_{21} = 2.297$, $P = 0.03$, same test).

Predation on flower heads.—Jumping spiders preyed on spiderlings in 26 (38%) of 69 eight-hour trials on *S. canadensis* and in 18 (27%) of 66 eight-hour trials on *S. juncea*. These frequencies did not differ significantly ($X^2_1 = 1.67$, $P > 0.1$ in a X^2 test). Predation occurred on average 177 ± 34.4 min. after release on *S. canadensis* and 173 ± 48.2 min after release on *S. juncea*. These predation times did not differ significantly, either ($t_{42} = 0.06$, $P > 0.9$).

Size vs predation risk.—No significant correlation took place between jumping spider size and predation times on *S. canadensis* (Fig. 2: $R^2_{1,24} = 0.019$, $P > 0.5$), but a significant inverse correlation took place on *S. juncea* (Fig. 3: $R^2_{1,19} = -0.271$, $P < 0.02$). On *S. juncea* large jumping spiders captured spiderlings more rapidly than did smaller ones. Thus, predation patterns differed with the substrate in jumping spiders of different size.

DISCUSSION

Time on the two goldenrods.—Spiderlings remained significantly longer on *S. canadensis* than *S. juncea*. Jumping spiders exhibited the same pattern, although staying for shorter times than the spiderlings on both substrates, probably a consequence of their different hunting strategies. Spiderlings are sit-and-wait predators (Morse 2007) that routinely remain for extended periods on satisfactory hunting sites, while jumping spiders are cursorial predators that roam continually (Jackson & Pollard 1996; Foelix 1996). The relatively long retention times exhibited by both species on *S. canadensis* strongly suggest a preference for *S. canadensis*.

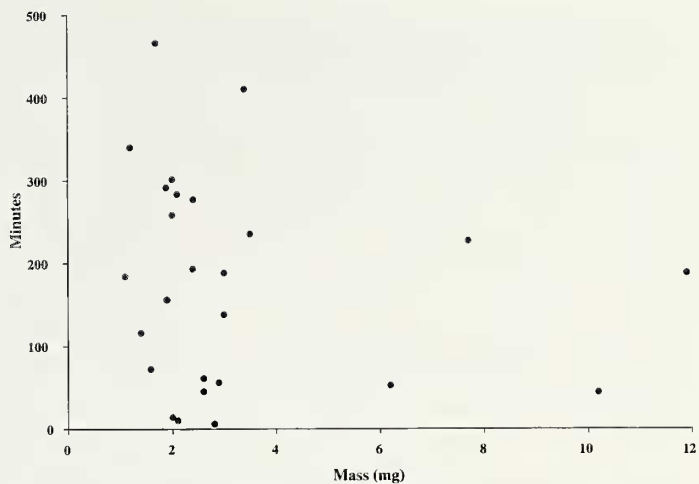


Figure 2.—Time for predation to occur vs. mass (mg) of jumping spider on the goldenrod *S. canadensis*.

These results suggest that predator avoidance plays a role in the substrate choice of the spiderlings, likely a response to the relatively rapid capture times by the large jumping spiders on *S. juncea*. They are also consistent with earlier studies showing that *M. vatia* on normal-density *S. canadensis* inflorescences initially spent much more of their time in hiding positions than did sibs on inflorescences thinned to about two-thirds normal density (Morse 2006), a density similar to that of *S. juncea*. The short capture times by the large jumping spiders on *S. juncea* suggest that they would frequently discover spiderlings on these sites in the field before quitting an inflorescence. These capture times of the large jumping spiders are also consistent with their capture patterns on the thinned *S. canadensis* inflorescences (Morse 2006), on which they maneuvered more easily than on the unthinned inflorescences.

Selection of flower heads.—The spiderlings leave their natal nests without maternal assistance (Morse 1992) and choose a substrate on their own. The significant choice of *S. canadensis* over *S. juncea* in the simultaneous choice experiment further supports the preference of *S. canadensis* by the spiderlings. The failure of the usually sedentary spiderlings to settle on the

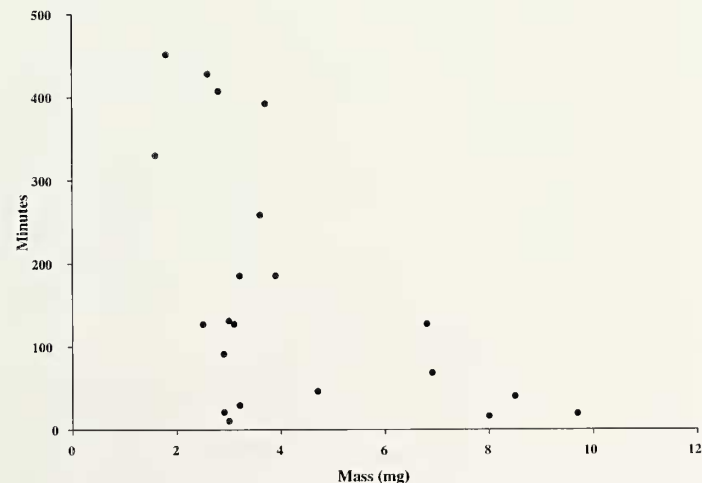


Figure 3.—Time for predation to occur vs. mass (mg) of jumping spider on the goldenrod *S. juncea*.

stems in the stem preference test suggests that their choice of *S. canadensis* does not result from tactile stimulation from the stem, although the stem is sometimes the first part of a goldenrod they encounter.

Previous studies have found no sign of *M. vatia* using chemical signals (LeGrand & Morse 2000; Anderson & Morse 2001; Leonard & Morse 2006), which renders an olfactory response to the vegetation unlikely, although not disproved. Information to date suggests tactile and/or visual cues as the best candidates, though the spiderlings do not discriminate among floral displays at distances of 10 cm (Morse 2005).

Predation on flower heads.—Predation times of the jumping spiders did not differ significantly on the two goldenrods, but they did demonstrate that large individuals were more effective on *S. juncea* than smaller ones. Although these predation setups do not closely match conditions in the field, they suggest that fine-level inflorescence structure may affect the vulnerability of the spiderlings to jumping spiders of different size.

It is important to consider variables controlled in the laboratory experiments that may affect safety on goldenrod in the field. The crab spiderlings' hiding positions in the field probably serve best in concealing them from passing predators as opposed to when confined for a considerable period in a small enclosure in the laboratory experiments. Jumping spiders have highly developed sight, making them formidable visual hunters (Jackson and Pollard 1996). The jumping spiders in this experiment had considerably more time to inspect the goldenrod branch containing the hiding spiderling than they would have in the field. However, if the preferred *S. canadensis* provided the safer hiding place, one would predict longer capture times on this substrate than on *S. juncea*.

This experiment compared jumping spider hunting performances on equal-sized branches of an inflorescence, not the entire inflorescences. Comparing same-sized branches of the two goldenrods may remove any potential safety advantage resulting from unequal sized branches routinely encountered in the field. Jumping spiders moved much faster than spiderlings, and when a jumping spider attacked a spiderling it captured the spiderling easily, even if the spiderling had hidden between the flower heads (Y. Garcia-Bengochea, pers. observ.). Thus, maneuverability within an inflorescence does not play an important role in predator avoidance by the spiderlings.

Prey visitation rates clearly did not play the central role in substrate choice by the spiderlings, since *S. canadensis* did not attract significantly more small insects than *S. juncea*. Although visitation rates of the spiderlings' major prey did not differ significantly, if these prey selected feeding sites on the basis of entire inflorescences, rather than on their density, the spiderlings might favor *S. juncea*, rather than *S. canadensis*, in that it attracted the most prey per inflorescence. At that rate, the spiderlings chose *S. canadensis* in spite of its slightly inferior prey-attracting ability.

Size vs. predation risk.—The significant inverse relationship between size of jumping spider and capture time on *S. juncea* suggests that *S. canadensis* is the safer substrate for spiderlings in the presence of large jumping spiders, and *S. juncea* is relatively safer for spiderlings in the presence of small jumping spiders. This result provides another test of the hypothesis that the spiderling's preferred substrate is the safer one.

Although we predicted that the small jumping spiders would have an advantage in finding and capturing spiderlings hidden in the dense goldenrod inflorescences, we found the opposite relationship on *S. juncea*. Inflorescences of *S. juncea* are less dense than *S. canadensis*, which may increase the predator's range of sight and/or maneuverability, giving the larger jumping spiders a better hunting opportunity and explaining the observed pattern. Earlier studies have revealed that when jumping spiders hunt large prey (relative to their own size), they will try to ambush the prey from behind (Jackson & Pollard 1996). The small jumping spiders may have been close enough in size to the crab spiderling to exploit this ambush technique under field conditions. However, the experimental setup did not allow the smaller jumping spiders (< 5 mg) to ambush their spiderling prey in this way, which may have prevented them from capturing the spiderlings more rapidly.

Implications at the community level.—How important are these interactions at the community level? They could easily drive the relative importance of jumping and crab spiders in the community level. As members of different hunting guilds (sit-and-wait vs. active hunter), these spiders may affect their principal herbivore prey in different ways. In an old field in Connecticut, Schmitz (2008) found that the relative abundance of sit-and-wait predators and hunters affected the impact of the commonest herbivore (a grasshopper), with the result that different grasses and herbs predominated in response to the different spider-mediated responses of the herbivores, and plant diversity and nitrogen mineralization ultimately varied as a result.

Our results thus support the hypothesis that subtle differences in inflorescence structure may play a major role in establishing the relationships among these important community members, and potentially the role of both species on herbivores and pollinators in old-field ecosystems. Millimeters matter! Not only do modest differences in size make a difference, but the sizes of the spiders change rapidly. This picture takes on added interest in that late-instar female *M. vatia* literally turn the tables and prey on *P. insignis* and other small jumping spiders (Morse 1992, 2006). These shifts are probably not unusual among old-field inhabitants (e.g., Persons et al. 2001). The spiderlings will also gain experience (Morse 2000b), a variable that we did not explore in this study because we used young, naive individuals. Lastly, the jumping spiders themselves have highly developed learning abilities (Harland & Jackson 2004) that may counter those of the spiderlings.

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